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GAMETIC COUPLING AS A CAUSE OF CORRELATIONS

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WHEN two distinct characters consistently occur together in the offspring of a hybrid, the phenomenon is termed in Mendelian parlance "gametic coupling." If the characters sometimes occur independently, but appear together more frequently than they should by chance, the term "partial gametic coupling" is applied. If the characters occur together less frequently than is to be expected, the condition is termed "repulsion," while if they never occur together in the same individual it is called "spurious allelomorphism."

In mathematical language, characters that show partial gametic coupling are said to be "positively correlated," those that show repulsion, "negatively correlated." If they always occur together in the same individual, the correlation is said to be "perfect" or "complete," while if they never occur together the negative correlation is perfect.

When characters that show a positive correlation or partial gametic coupling are derived from the same parent, they are termed "coherent" by Cook (1909, p. 16). Many of the examples of partial gametic coupling formerly reported in Mendelian literature were probably of this nature, but with the attention focused on the idea that all characters were independent units, the possibility of such coherence was not considered, and it is sometimes

not to be determined from the data presented whether the correlated characters were derived from the same or different parents. This phenomenon of coherence, which appears to most field naturalists and practical breeders as a well-known fact, strikes the followers of Mendel as a novel idea, to judge from the following (Bateson & Punnett, 1911, p. 6):

> The fact, however, that the mode in which factors are combined in the original parents can influence the distribution of the factors among gametes of F_1 introduces a new conception into genetic physiology.

The difficulty of "breaking up" combinations of characters has so long been a stumbling block to breeders that to them the conception can hardly be considered new. The suggestion that the number of individuals in which two characters are combined bears a definite relation to the number in which they occur singly is without doubt a direct outgrowth of Mendelian investigations and methods of thought. Perhaps this latest application of mechanical conceptions to biology may stimulate research as did Mendel's original discovery. On the other hand, there are many who think that the application of Mendelian formulæ has already been pursued to an absurd point by the factoring and subfactoring of characters and the assumption of intensifying and inhibiting determinants. Those not already abreast of Mendelian literature are not likely to be impressed with the further refinement that aims to devise formulæ for expressing gametic relations between two of these already complicated Mendelian systems.

In considering the relation between two Mendelian characters four possible combinations are involved. Thus, if *A* and *B* be taken to represent the appearance of the two characters, and *a* and *b* their non-appearance, these four combinations would be expressed as follows: *AB*, *Ab*, *aB*, and *ab*. The theory of gametic coupling assumes that an attraction or other unknown relation exists between the determinants of the two characters,

which results in their occurring together in gametes more frequently than they occur separately.

There appears to have been a preconceived idea that the ratio between the number of gametes in which the determinants for two characters occurred together and the number in which they were separated would be either as 3:1, or 7:1, or 15:1, ratios that are common in Mendelian inheritance of single characters. The reason for this expectation is not apparent.

The persistence with which it is sought to utilize the numbers 4, 8, 16, etc., representing powers of 2, in the interpretation of correlations reminds one of the arguments used at the dawn of science to bring all natural phenomena into some relation with the numbers 4 and 7. Galileo's suggestion that there were more than seven planets was answered by Lizzi:

> There are seven windows in the head, two nostrils, two eyes, two ears, and a mouth, so in the heavens are there two favorable stars, two unpropitious, two luminaries, and Mercury alone undecided and indifferent. From which and many other similar phenomena of nature, such as the seven metals, etc., which it were tedious to enumerate, we gather that the number of planets is necessarily seven. (Snyder, 1907, p. 203.)

The levity of the comparison disappears when one seeks a reason for assuming that the number of gametes in which the characters occur together will be to the number of gametes in which they occur apart as 7:1 or 15:1 or 31:1, etc., and not some intermediate proportion.

In the following pages an attempt is made to review briefly the experiments which have been advanced as proof that the various degrees of correlation fall into this definite series.

The first attempt to refer the correlation of characters to definite differences in the gametes was made by Bateson, Saunders, and Punnett (1906, p. 9) in explaining observed correlations between purple flower color and long pollen grains in hybrid sweet peas.

> . . . A close approach to the Observed F_2 numbers would be given

by a system in which each 16 gametes were composed, thus: $7AB + 1aB + 1Ab + 7ab$, where A is long pollen and a round pollen.

	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
Observed	1,528	106	117	381	1,199	394
Calculated	1,448.5	122.7	122.7	401.5	1,220.5	407.4

The numbers under "White" may be disregarded in this connection since the distribution of long and round pollen grains in this group shows a close approach to the normal 3:1 ratio.

Some of the numbers in the "observed" series are above and some below the corresponding numbers of the "calculated" series. That the calculated series approximates the observed series is obvious, but there is no way of determining the degree of this approximation. No method has been proposed for making definite comparisons between such series of numbers. Without some standard of comparison it is difficult to see that anything is gained by resorting to gametic formulæ to represent the degrees of association between characters.

A customary and direct method of comparing the degrees of relationship that exists between any two characters is to compute the coefficient of correlation or Yule's "coefficient of association."

In the following discussion Yule's "coefficient of association" (1900) is used. By this method the complete independence of two character pairs is represented by 0, complete association by 1. Intermediate degrees of relationship are expressed by the intermediate decimals. If the four classes of individuals are represented by a, b, c and d, the coefficient of association is

$$\frac{(a \times d) - (b \times c)}{(a \times d) + (b \times c)}$$

Since this coefficient can be computed directly from the observed numbers the predication of gametic formulæ as a means of expressing degrees of association of characters becomes unnecessary.

With relationships expressed as coefficients of association, probable errors can be calculated. Thus it becomes possible to determine whether the approximations between observed ratios and those calculated from the different gametic formulæ are closer than would result from chance.[1]

The difficulty of securing a 7:1 distribution by dichotomous cell division was appreciated by Bateson and his collaborators in the example first cited. The possibility that the coupling was in an 8:1 ratio was also suggested and kept in mind for a time until a grouping that approximated that resulting from a gametic coupling of a 15:1 ratio was obtained. Regarding the choice between the 7:1 and 8:1 ratios to explain the numbers observed in the first experiment, the authors remarked (Bateson, Saunders and Punnett, 1908, p. 3):

> . . . we are still unable to decide finally between them.

But this indecision was apparently overcome in a subsequent paragraph on the same page. After citing two examples that were referred to a 15:1 ratio, the theory that the couplings follow a definite series was launched in the following statement:

> The undoubted existence of these two grades of gametic coupling in the Sweet Pea suggests that each may find its place in a scheme of increasing intensity of gametic coupling, such as is shown in the accompanying table, where the two allelomorphic pairs are represented by *Aa* and *Bb*:

[1] Heron has pointed out (1911, p. 109) that the results secured by Yule's formula for the "coefficient of association" do not approximate the true coefficient of correlation, except where the two divisions are near the mean of the entire population. This condition is not met, of course, by characters that occur in one fourth and three fourths of all the individuals. But since the present discussion is confined to examples that approximate the form $3n^2-(2n-1):2n-1:2n-1:n^2-(2n-1)$, where $2n$ = the number in the gametic series, they afford a regular sequence and, though the actual values are somewhat arbitrary, they should not be misleading as a means of comparing the degrees of relationship represented by the different gametic formulæ. Thus if the classes observed in an experiment show the same coefficient of association as the classes calculated from some particular gametic ratio, the two series will also give the same coefficient of correlation, though the actual values may differ.

Gametic Series *AB* *Ab* *aB* *ab*	Zygotes Containing *A* and *B*	*A* only	*B* only	Neither *A* nor *B*	
1 : 1 : 1 : 1 = 4	9	: 3 :	3 :	1	= 16
3 : 1 : 1 : 3 = 8	41	: 7 :	7 :	9	= 64
7 : 1 : 1 : 7 = 16	177	: 15 :	15 :	49	= 256
15 : 1 : 1 : 15 = 32	737	: 31 :	31 :	225	= 1,024
$n-1 : 1 : 1 : n-1 = 2n$	$3n^2-(2n-1)$	: $2n-1$:	$2n-1$:	$n^2-(2n-1) = 4n^2$	

The first term in the series is a simple case of dihybridism in which no coupling exists. The second term we have not yet encountered. But we have an ample series of experimental data which satisfy the third term; and the experimental evidence for the existence of the fourth term rests upon two independent cases.

To facilitate the use of the coefficient of association as a means of determining what gametic ratio most closely approximates observed ratios, Table I has been prepared. This table shows a series of gametic ratios in which the less frequent combinations are taken as 1, and the resulting zygotic series, with the number of individuals that would occur in each of the four classes, followed by the coefficient of association, calculated from the numbers in the zygotic series. The ratios in heavy type are those representing the powers of two to which correlations have been referred under the theory of gametic coupling.

TABLE I

RATIOS OF GAMETIC COUPLING

Gametic Series	Zygotic Series	Coefficient of Association
1 : 1 : 1 : 1	9 : 3 : 3 : 1	.0
2 : 1 : 1 : 2	22 : 5 : 5 : 4	.558
3 : 1 : 1 : 3	**41 : 7 : 7 : 9**	**.766**
4 : 1 : 1 : 4	66 : 9 : 9 : 16	.858
5 : 1 : 1 : 5	97 : 11 : 11 : 25	.905
6 : 1 : 1 : 6	134 : 13 : 13 : 36	.932
7 : 1 : 1 : 7	**177 : 15 : 15 : 49**	**.949**
8 : 1 : 1 : 8	226 : 17 : 17 : 64	.961
9 : 1 : 1 : 9	281 : 19 : 19 : 81	.969
10 : 1 : 1 : 10	342 : 21 : 21 : 100	.975
11 : 1 : 1 : 11	409 : 23 : 23 : 121	.979
12 : 1 : 1 : 12	482 : 25 : 25 : 144	.982
13 : 1 : 1 : 13	561 : 27 : 27 : 169	.985
14 : 1 : 1 : 14	646 : 29 : 29 : 196	.987
15 : 1 : 1 : 15	**737 : 31 : 31 : 225**	**.988**
16 : 1 : 1 : 16	834 : 33 : 33 : 256	.990
31 : 1 : 1 : 31	**3,009 : 63 : 63 : 961**	**.9973**
63 : 1 : 1 : 63	**12,161 : 127 : 127 : 3,969**	**.9993**
127 : 1 : 1 : 127	**48,897 : 255 : 255 : 16,129**	**.9998**

Returning to the consideration of the original example of gametic coupling in the sweet peas, the coefficient of association, $.958 \pm .004$, is seen to be intermediate between that resulting from a 7:1 and an 8:1 ratio.

Notwithstanding the fact that the figures correspond somewhat more closely with an 8:1 than they do with a 7:1 ratio, an evident preference for numbers that are powers of 2 is shown when the possibility of an 8:1 ratio is discussed. Instead of saying that 18 gametes are concerned, the number is spoken of as $16 + 2$, and the fact that a ratio of 15:2 would give almost exactly the observed association is not even considered.

The next example of gametic coupling to be reported was in the same series of crosses (Bateson, Saunders and Punnett, 1908, p. 11), where the progeny of four individuals showed the following grouping: 296:19:27:85. This is referred by the authors to the theoretical 7:1 ratio, though it shows almost the same association as an 8:1 ratio, that is, .960. The probable error, .008, would indicate, however, that with this number of individuals such a deviation might easily be due to chance. The numbers are, therefore, too small to afford evidence affecting the choice between a 7:1 and an 8:1 formula.

From the progeny of one of these four individuals consisting of 111 plants and showing an association of .914, 10 individuals showing both dominant characters were selected and propagated. The progeny of the 10 plants taken together gave the following grouping: 493:25:25:138. This grouping is considered only in connection with the 7:1 and 15:1 distribution, though the association $.982 \pm .004$ would indicate that a gametic series of 12:1 would most closely fit the numbers. The deviation from the 7:1 ratio is 9 times the probable error, and from the 15:1 ratio, about twice the probable error.

With respect to the characters considered separately, the classes secured from each of the 10 individuals showed a remarkable conformity to the expected 3:1

ratio. In the degree of association between the characters, however, no such uniformity was exhibited. Leaving out of consideration two families represented by only a few individuals, the coefficient of association varies from .910 to .990. In terms of gametic coupling this shows a range from 6:1 to 16:1, and since the series as a whole accords with a 12:1 ratio it is not apparent why only 7:1 and 15:1 ratios are considered.

Individuals were again selected from two of the families which showed the highest correlation, and grown the following season. The progeny from the first family behaved irregularly and the presence of some disturbing process was suspected, though the deviations with respect to the individual character pairs were less than the probable error.

The second family gave individuals with the following grouping (Bateson, Saunders and Punnett, p. 12): 583:26:24:170 (association $.987 \pm .0026$). Of this it is said:

> It is obvious that the numbers in this group of families accord very closely with the figures expected on a 15 : 1 : 1 : 15 basis, and the view that this is the system actually followed receives confirmation from the distribution of the pollen and color characters in F_2 families from the Bush $\times$ Cupid crosses where the following figures were obtained: 131:6:5:42. (Association $.989 \pm .005$.)

Here again when it is said that the figures "accord very closely," it can only be meant that they accord closely with one of the formulæ in the hypothetical series as compared with other members of the series. The numbers are, of course, inadequate to afford evidence as to whether the observed figures accord more closely to those resulting from a 15:1 combination than they do, for example, to a 16:1 or a 14:1, yet the results are taken to support the original assumption that the groupings are in powers of two.

The examples of gametic coupling thus far reported are summarized by Bateson and Punnett as follows (1911, p. 5):

3:1. No case yet known.
7:1. *Sweet Pea.* Blue factor and long pollen.
7:1. *Primula sinensis.* Magenta color and short style.
15:1. *Sweet Pea.* Fertile anthers and dark axils.
31:1. No case yet known.
63:1. *Pisum.* Development of tendrils and round seed.
127:1. *Sweet Pea.* Blue factor and erect standard.

As we have seen, the first example is closer to an 8:1 ratio. The second example is apparently based on an experiment comprising 47 individuals (Gregory, 1911, p. 12). The classes were 33:3:1:10, and the author states,

> . . . the partial coupling observed is almost entirely certainly of the form 7 : 1 : 1 : 7.

The reason for this assurance is not apparent since the grouping is really nearer to that resulting from a 15:1 ratio. The probable error, .015, is so large, however, that it would be impossible to determine the grade of coupling closer than to say that it probably falls somewhere between 8:1 and 31:1.

The third example referred to the 15:1 ratio appears to be based on 885 individuals showing an association of $.993 \pm .0017$, indicating a coupling of about 20:1, the deviation from the 15:1 association being 2.9 times the probable error.

With respect to the examples where the association is closer, none of the reported experiments have been conducted on a sufficient scale to determine whether the gametic ratios that are multiples of two are approximated more closely than other ratios. One of the most exact approximations thus far reported is that of Vilmorin and Bateson (1911, p. 10) where the numbers 319:4:3:123 (association $.9994 \pm .0003$) were obtained. This is certainly a close approximation to the figures that would result from a gametic coupling of 63:1:1:63, which for this number of individuals would be 333.27:3.48:3.48:108.77. Yet the observed numbers can be still more closely approximated by assuming that the coup-

ling was in the proportion of 75:1, which would give the figures 334.57:2.98:2.98:109.47. The observed numbers are somewhat closer to the 63:1 than to the 127:1, the proportion next above in the proposed series. But why avoid the intermediates?

It should be kept in mind that the series was built up in the first place, not because the observed numbers agreed with some member of this series more closely than was to be expected by the laws of chance, but apparently for *a priori* reasons, because the numbers in this series were in accord with the Mendelian ratios for the appearance of single characters which represent powers of 2.

When the correlation is as high as in the above example it would require, not hundreds of individuals, but tens of thousands to prove that the observed numbers were in accord with those resulting from any particular gametic ratio. In the experiment referred to the 63:1 ratio, there are two classes represented by 4 and 2 individuals, respectively. A change of two or three individuals in each of these classes would cause the array to correspond as closely with a 31:1 or 127:1 ratio as it now does with the 63:1.

In the very nature of things any observed association must fall nearer to some one of the calculated ratios than to any other, yet in the discussion of these experiments this seems not to have been appreciated. The data would have supported in the same way any other choice of preferred ratios.

COHERENT CHARACTERS IN HYBRIDS OF CHINESE MAIZE

Beginning in 1908, experiments have been conducted with a variety of maize secured from China. The endosperm of this Chinese variety is of a peculiar waxy texture, a character thus far not reported in any other variety.

There are two strains of the Chinese variety, one white, the other with colored aleurone. In a series of

hybrids between Chinese and American varieties made by Mr. J. H. Kempton and the author, the waxy character was found to be definitely recessive in the first generation. In the second generation the character reappears apparently unchanged in slightly less than 25 per cent. of the individual seeds.

Crosses between white Chinese and colored American, and colored Chinese and white American showed a pronounced coherence between the texture of the endosperm and the color of the aleurone layer.

Results of the first season's work in this field were reported at the International Conference of Genetics in Paris, 1911. At that time no attempt was made to determine the gametic ratios necessary to account for the observed correlations.

In these crosses the characters segregate with definitely alternative expression, but the classes seldom show simple Mendelian ratios. In only one cross were two of the four classes even approximately equal.

In the results of the next season's work there were five additional ears sufficiently near the 3:1 ratio in both characters to be considered from the standpoint of gametic coupling. The data derived from these five ears, and from the one of the previous season, are shown in Table II.

TABLE II

Ear No.	No. Seeds	Colored Horny	Colored Waxy	White Horny	White Waxy	Coefficient of Association	Deviation from Coefficient of 3:1 Ratio	Deviation in Terms of Probable Error
152	183	112	20	22	29	.761 ± .049	.005	0.10
301	579	372	62	63	82	.773 ± .029	.007	0.24
302	536	343	52	53	88	.833 ± .024	.067	2.79
303	627	409	57	62	99	.839 ± .021	.073	3.48
325	650	434	55	61	100	.856 ± .019	.090	4.74
380	161	104	17	18	22	.764 ± .058	.002	0.03
Total	2736	1774	263	279	420	.821 ± .011	.055	5.00

The ratios obtained in these six cases might be hailed as a prediction fulfilled, since in every case the numbers approximated those that would result from a 3:1:1:3 ratio, which has remained a gap in the theoretical series.

In three of the six ears the deviation from the correlation resulting from a 3:1 ratio is less than the probable error. The deviation for the total is less than three times the probable error, and might readily be only a chance deviation. In two of the ears, however (Nos. 303 and 325), the deviations are rather large to be ascribed to chance.

In view of the fact that previously reported experiments fail to show an equally close approximation to other members of the proposed series, there is no adequate reason for assuming that the present approximation to the numbers of a 3:1 ratio belongs to a series of formulæ represented by the powers of 2. That no such regularity exists in the interrelation of different character pairs is more definitely demonstrated by the experiments described below. These results indicate that the association of characters may be determined after the conjugation of the gametes.

COHERENCE OF CHARACTERS NOT ALWAYS THE RESULT OF GAMETIC DIFFERENCES

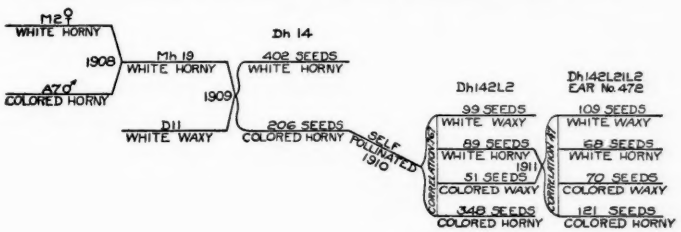
If correlations are in all cases due to gametic differences, there should be no correlations exhibited in a cross with a Mendelian formula $Aabb \times aabB$. In our experiments with corn this would be represented by a cross between colored-waxy and white-horny, where the first is heterozygous in aleurone color and the second heterozygous in endosperm texture. The colored aleurone is dominant to white, and the horny endosperm to the waxy. If colored aleurone is represented by C, white aleurone by *c*, horny endosperm by *H*, and waxy endosperm by *h*, the gametic structure would be as follows: Female parent, *cchH*, producing two classes of gametes, *ch* and *cH*; male parent, *Cchh*, producing gametes *Ch* and *ch*. In neither case is there opportunity for coupling in the gametes since in the female parent all of the gametes should bear the white character, and those of the male parent the waxy character. The sig-

nificance of crosses of this nature was not realized at the time pollinations were being made, and but 5 ears of this kind were secured. In two of these ears there is a significant correlation. The classes exhibited in the five ears are shown in Table III.

TABLE III

Ear No.	No. Seed	Per Cent. White	Per Cent. Waxy	White Waxy	White Horny	Colored Waxy	Colored Horny	Coefficient of Association
472	505	30.1	46.4	91	61	143	210	.373 ± .057
471	368	48.	48.6	109	68	70	121	.47 ± .056
314	283	44.5	52.7	65	61	84	73	−.038 ± .081
272	395	61.2	47.1	122	120	64	89	.171 ± .068
256	141	46.8	48.9	27	39	42	33	−.295 ± .105

The two ears in which the correlation appears significant (Nos. 471 and 472) have a common ancestry, different from that of the other ears. The history of these ears is as follows: In 1908 a plant of a white Mexican variety was pollinated by a Hopi variety with colored aleurone, producing a pure white ear, *Mh*19. In 1909 a plant from *Mh*19 was pollinated by white Chinese, the variety possessing the waxy endosperm. The resulting ear *Dh*14 had white and colored seed in the proportion of 2 white to 1 colored, with no trace of the waxy endosperm. In 1910 a plant from a colored seed of *Dh*14 was self-pollinated, producing an ear *Dh*142*L*2 with the fol-



lowing classes: white-waxy 99, white-horny 89, colored waxy 51, colored horny 348. This represents an association between colored and horny of .767, almost exactly that expected on a coupling ratio of 3:1, but it will be

noticed that the two middle classes are not equal. In 1911 two plants grown from white horny seeds of *Dh*142*L*2 were pollinated by a plant from a colored waxy seed of the same ear, producing the two ears, Nos. 471 and 472. The pedigree of these two ears is graphically shown in Diagram 1.

The plants which bore ear 472 bore also a second ear which was self-pollinated. Contrary to expectation, this ear showed slight traces of aleurone color. That there was a tendency to produce aleurone color in this extracted recessive is also indicated by the low percentage of the total white seeds in ear 472, which is 30 instead of 50.

With ear 471 there is every indication that one of the parents was homozygous with respect to the recessive color character and the other with respect to the texture of the endosperm. A self-pollinated second ear from the plant that produced ear 471 had 24 horny seeds and 5 waxy, all of them white. A self-pollinated ear was also secured from the plant which was the male parent of both 471 and 472. This ear had 31 white seeds and 128 colored, all of them waxy. The total percentage of white seeds in ear No. 471 was 48, a close approximation to the expected 50.

The nature of this experiment seems to preclude the application of the theory of gametic coupling which would explain correlations by assuming attractions or repulsions between the character determinants in the gametes. While attractions which might cause some combinations to be represented by larger numbers of gametes would disturb the Mendelian ratios, they could not produce the effect of correlation or coherence of characters.

Thus the female parent might produce more gametes bearing white and waxy than it did colored and waxy, or there might be a greater fatality among the colored waxy gametes. Any such disparity in the classes of the gametes would result in more than 50 per cent. of

the zygotes showing the recessive characters, but even so, there would be no correlation.

On the presence and absence hypothesis, a positive correlation between two dominant characters like aleurone color and horny texture must be considered a different phenomenon from a positive correlation between color and waxy texture (Bateson, 1909, pp. 151, 158). The first case has to be looked upon as an example of attraction, the second of repulsion. This appears an unnecessary complication, as Emerson (1911, p. 79) has pointed out. The significant fact would seem to be that both cases may be considered as examples of coherence.

Appreciation of the fact that many of the cases of gametic coupling are examples of coherence makes any assumed regularity in the degree of correlation still more absurd. But in spite of cases of coherence that result in reversal of correlation, the idea that the characters are represented by material particles that remain unchanged by association in the zygote continues to be held. To preserve the conception of pure unit characters, theories of positional relations of unit characters are now being proposed. Simple Mendelian ratios can also be explained by positional relations of character determinants as well as by theories of alternative transmission (Swingle, 1898; Cook, 1907, p. 353), and this view has the advantage that it can accommodate facts which indicate a complete transmission of characters.

A theory to explain how positional relations of determinants in the chromosomes may be responsible for the phenomenon of coherence has been proposed by Morgan (1911). The suggestion is that coupled or positively correlated characters may lie close together in the chromosome and that in the conjugate generation pairs of chromosomes are twisted around each other. If, as claimed, the chromosome pairs split in a single plane, characters which lie close together in the original chromosomes would seldom be separated, while characters remote from each other in the chromosome would stand an even chance of being separated.

If the position of the various determinants in the chromosomes is definite, only slight variations in the degree of association among hybrids between the same parental strains would be expected, but there would be no reason to expect that the different degrees of correlation should fall into a definite series.

SELECTIVE POLLINATION

From the standpoint of complete segregation or alternative inheritance of characters there remains the possibility of correlations being the result of selective pollination. It is conceivable that the ovules which bear one of the segregating characters are more readily fertilized by pollen bearing another character with which it was associated in the parent. As applied to our own experiments, ovules which are potentially waxy might be more readily fertilized by pollen which is potentially white.

If correlations are the result of selective pollination, no correlation should be shown as the result of crossing an individual that is heterozygous with respect to both of the character pairs with an individual showing both of the recessive characters, for in such a cross the gametes of one parent would be all of one kind. In our own experiments, crosses between plants from hybrid seed showing horny endosperm and colored aleurone (both dominant characters) with plants from white waxy seeds (both recessive characters) should throw light on this point.

If the correlations result from numerical inequalities in the classes of the gametes, the seed classes resulting from such a cross as that described above should be the same as the gametic classes produced by the heterozygous parent. Thus, if the seed classes in a self-pollinated ear correspond to those expected from a 3:1 ratio, the same plant when crossed with a plant showing both recessive characters should show classes in the ratio, 3 white-waxy, 1 white-horny, 1 colored-waxy, and 3 col-

ored-horny. On the other hand, if the correlations result from selective pollination, no correlation should appear in such a cross since the pollen is all of one kind. Ears that represent crosses of this kind are described in Table IV. It will be seen that in all of the seven ears there is a significant correlation.

TABLE IV

Ear No.	No. Seeds	Colored Horny	Colored Waxy	White Horny	White Waxy	Coefficient of Association
144	600	125	40	232	203	.464 ± .054
250	245	19	74	104	48	−.788 ± .040
251	377	52	29	138	158	.345 ± .077
390	458	115	35	94	214	.764 ± .032
391	231	65	10	49	107	.868 ± .032
392	316	84	16	68	148	.840 ± .051
401	518	3	29	263	223	−.839 ± .061

It is interesting to note that in two ears, Nos. 250 and 401, while the correlation is relatively high, it is reversed; *i. e.*, the positive correlation is between colored aleurone and waxy endosperm instead of between colored aleurone and horny endosperm as was the case in the original F_2 ears. Whether the correlation is positive or negative does not affect its use as evidence in eliminating the possibility of selective pollination, so long as the correlation is significant. From the standpoint of the presence and absence hypothesis, the coupling or attraction has given place to a repulsion.

The results shown in Tables III and IV indicate that the association of different characters may be determined at different stages in the ontogeny of the individual, much as the appearance or non-appearance of a simple character may occur at different times in the life history. Thus in ears 471 and 472, Table III, the correlated characters must have become associated after the formation of the gametes, while the absence of positive correlation in ears 314 and 317 of the same table shows that in these ears where associations in the gametes were excluded no correlations were subsequently produced. The results in Table IV further show that excluding the

possibility of selective pollination did not prevent the appearance of significant correlations. It appears no more reasonable to assume that the number of individuals that are to show a particular combination of characters is always determined at the time the gametes are formed, than it would be to argue that the number of nodes destined to bear a juvenile type of foliage are definitely determined at this time.

The theory of gametic coupling advanced by Bateson and Punnett leads them (1911, p. 6) to entertain the idea that, while segregation is definite and complete, the apparently significant cytological processes of maturation may have nothing to do with the phenomenon. These authors would have the association of characters determined before the maturation divisions.

> Now that we know of a series involving as many as 256 terms (127 + 1 + 1 + 127) it is most difficult to conceive that such a system can be produced in the maturation-divisions of the ovarian tissue of such a plant as a sweet pea. We may well be tempted to look much earlier in the developmental processes for the establishment of these differentiations, and it is not impossible that they may be established as early as the embryonic constitution of the sub-epidermal layer itself.

The suggestion that segregation occurs early in the ontogeny of the individual was apparently occasioned by the belief in the definiteness of the mathematical relations between different character pairs. As we have seen, there is little evidence for this belief. The correlation shown in ear 471, Table III, affords a definite indication that such associations of characters may be formed after the production of the gametes.

Even though the definite and material segregation of characters be maintained, all grades of correlation could still be determined during the two nuclear divisions that follow synapsis. The process might be looked at as follows:

When two character pairs are involved in a hybrid, the tetrads resulting from the different mother cells would

all be of three types with respect to the two characters involved: (I) *AB, AB, ab, ab;* (II) *AB, Ab, ab, aB;* (III) *Ab, Ab, aB, aB.* Each of these fulfills the condition deemed necessary from a Mendelian standpoint, that two daughter cells of each tetrad receive the dominant and two the recessive determinants. Where *A* and *B* are correlated, it may be assumed that tetrads represented by (III) are not formed. If the two remaining kinds were produced in equal numbers, a gametic ratio of 3:1:1:3 would result. By the formation of two mother cells of type I for every one of type II, a ratio of 5:1:1:5 would result. The formation of these two types of mother cells in different proportion would provide for all degrees of correlation.

Additional examples of gametic coupling, some of which, at least, are in the nature of coherences, are reported by Gregory (1911, *B*, p. 128). As in our experiments with hybrids of Chinese maize, examples of gametic coupling were encountered of a lower order than 3:1:1:3, the lowest ratio in the theoretical series. Even this discovery did not result in his questioning the validity of the hypothesis. A further refinement was devised to accommodate the results. Advantage was taken of the possibility that the gametic coupling may exist in only one sex:

> For the time being it may be pointed out that a very close approximation to the observed numbers is given by the assumption that a coupling of the form 7 : 1 : 1 : 7 is present in gametes of one sex only, gametes of the opposite sex being produced in equal numbers of all four kinds.

In such a case, a gametic coupling of the 7:1 in one sex, with all classes equally represented in the other sex, would result in an association of .542, slightly lower than that resulting from the ordinary 3:1 ratio. By a similar fractioning of the 3:1 ratio, the series can be provided with a still lower member, with an association of .390.

In all recently reported experiments the reality of the

proposed series of ratios seems to be taken for granted and results are viewed only from this standpoint.

It is hoped that the previous discussion may operate to check this practise of referring examples of coherence to preconceived gametic ratios without considering the possibility that an apparent agreement may be only a chance approximation.

So long as the preconceived series is taken for granted and intermediates are not considered, the results of all experiments will seem to give additional evidence in support of the series.

We have seen that the results of previously reported experiments do not correspond to the ratio in the expected series more closely than they do to others that are intermediate, and furthermore that in some cases, at least, the associations are not due to relations of the determinants inside the gametes at all, but occur after the stage of karyapsis, or nuclear fusion, has been reached (Cook and Swingle, 1905).

SUMMARY

The theory of gametic coupling assumes that correlations between two Mendelian character pairs are caused by attractions or repulsions between character-units or determinants, previous to the formation of the germ cells. These attractions or repulsions are supposed to increase the number of gametes bearing certain combinations of determinants.

The further assumption that the various degrees of association observed between different character-pairs will fall into a regular series represented by powers of 2, as in simple Mendelian hybrids, appears to have been accepted without adequate analysis of the data on which it was based.

An examination of the early examples shows that it was only by neglecting the possibility of intermediate ratios, and thus begging the question, that the observed

numbers could be said to agree with those of the proposed series.

The lack of any standard or method for making quantitive comparisons between observed and expected series has made it impossible to determine the degree of the supposed approximations. Yule's coefficient of association is proposed as a criterion of comparison, and to make possible the determination of probable erors.

In several cases correlations have been found to be reversible, depending on the way the characters were combined in the parents. This fact has further complicated the theory of gametic coupling, making it necessary to assume that characters which at one time attract each other, at others exhibit repulsion.

In hybrids between Chinese and American varieties of maize coherence has been found between the texture of the endosperm and the color of the aleurone layer. In a few cases, the degree of the correlation approached very closely to that expected from a gametic coupling in a 3:1 ratio (Table II).

Correlations were found in crosses of the Mendelian form $Aabb \times aabB$ (Table III). Such correlations are held to indicate that in some cases at least, the correlation between the characters must be determined after the formation of the gametes.

On the other hand, correlations resulting from crosses of the form $AaBb \times aabb$ eliminate the possibility of selective pollination as a general cause of correlations (Table IV).

The general conclusion is reached that associations between characters, like the appearance of single characters, may rise at different stages in the ontogeny of the individual.

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March, 1912

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MICE: THEIR BREEDING AND REARING FOR SCIENTIFIC PURPOSES[1]

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I. INTRODUCTION

NOTWITHSTANDING many shortcomings mice have contributed much to the advancement of science and the service of mankind. To realize this we have but to recall that it was by crossing the white with the gray mouse that Mendel's Law of Inheritance was first found to apply to the animal kingdom (1); that from a study on mice some of the earliest concepts of immunity were obtained (2); and that from experiments now in progress on them an insight is being gained into the nature of cancer (3). These and similar experiments indicate something of the scope to which these animals have been put.

The ease with which white mice can be handled makes them, in many ways, preferable for experimentation to other and larger rodents. But, owing to a widespread notion that they are difficult to rear under laboratory conditions, their usefulness has been greatly curtailed.

The method usually employed in the breeding of mice has been what we may term extensive. By this I mean that many animals are kept from which to obtain offspring. I have set myself the task of breeding mice intensively, that is, of keeping relatively few, but of keeping these under conditions which will insure their productivity. It is the purpose of this paper to describe the way in which this was done.

II. THE INTENSIVE BREEDING OF MICE

A. Detrimental Factors

1. *Marked Fluctuations in Temperature.*—Probably no single factor is more likely to be overlooked than that mice, to produce to the best advantage, require an equable temperature. While they can withstand extremes

[1] From the Zoological Laboratory, University of California.

of heat or cold, such extremes are not conducive to their productivity. At 35° C. I have found breeding to be greatly impeded, and at a temperature as low as 2° C. the young born are subject to a number of mortal ills which practically prevent their reaching maturity. But a constant temperature of either of the above extremes is not so detrimental as is great fluctuation in temperature. A mouse taken from favorable conditions and subjected to daily fluctuations of from 30° C. to 2° C. soon becomes a different animal physiologically. The fur which was sleek and glossy roughens, the exposed veins in the ears and tail darken, and the animal is readily reduced to a condition which, if prolonged, not infrequently terminates in death. If after having reached this condition, however, the animal be promptly restored to equable conditions of temperature, its fur becomes sleek, signs of anæmia disappear and the mouse regains its normal health and vigor often with surprising rapidity.

2. *Parasitism.*—If mice, even under the most favorable conditions of temperature, become badly parasitized breeding ceases and unless they are ridded of the parasites the adult mice as well the young fall victims to this pest. To test the effects of parasitism, I have taken mice from fresh stock, kept under excellent conditions, and have placed them in infested nests, with the result that in a few days the mice became sluggish, and many sooner or later died.

When the two factors—parasitism and wide fluctuations in temperature—are combined, the animals, especially the young, die in great numbers.

B. Factors Essential to Intensive Breeding

1. *Construction and Equipment of Cases.*—In general, where a number of mice are to be kept together, the wire and wood cases described by Yerkes (4) has been much used. But for intensive breeding I have found it better to keep few mice in a case, and to keep these under better conditions of sanitation than is possible in the above case.

I know of no better plan to insure sanitation than to construct cases which will offer little surface upon which

dirt may collect, and which at the same time will make evident that which has accumulated. Such a case should be made with a perforated bottom and should be pro-

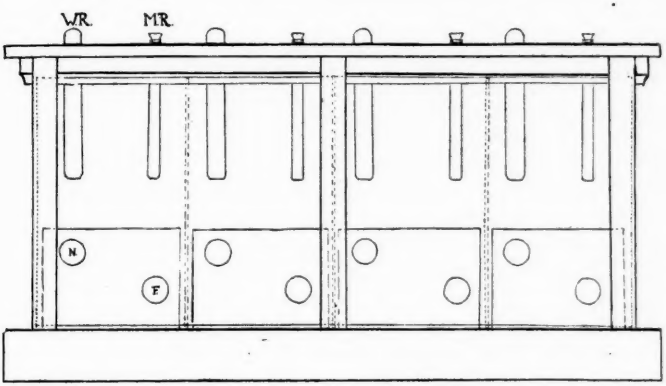

FIG. 1. FRONT VIEW OF CASE. *W.R.*, water receptacle; *M.R.*, milk receptacle; *N*, entrance to nest; *F*, opening to food.

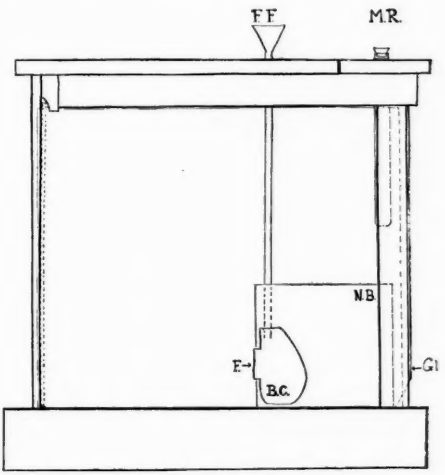

FIG. 2. END VIEW OF CASE. *FF*, food funnel; *M.R.*, milk receptacle; *N.B.*, nest box; *Gb*, galvanized iron back (near its bend); *F*, entrance to food cup *BC*.

vided with sides of glass. Briefly described,[2] the case that I have constructed consists of a framework of light wood, a back of galvanized iron and sides, front and par-

[2] For detail see description accompanying drawings of the case.

tition of 10 × 12 glass. The top is made of screen wire; the bottom of ¼ inch wire mesh (hardware cloth).

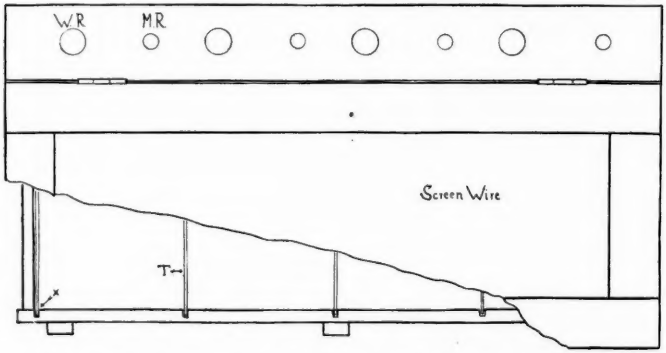

FIG. 3. TOP OF CASE, WITH A PART REMOVED TO SHOW HOW THE GLASS PARTITIONS AND ENDS (*X*) ARE FIXED INTO THE FRAME. *WR.*, water receptacles; *T*, a bent piece of tin covering the upper end of the glass to increase the height of the partition and at the same time to cover the sharp edge of the glass.

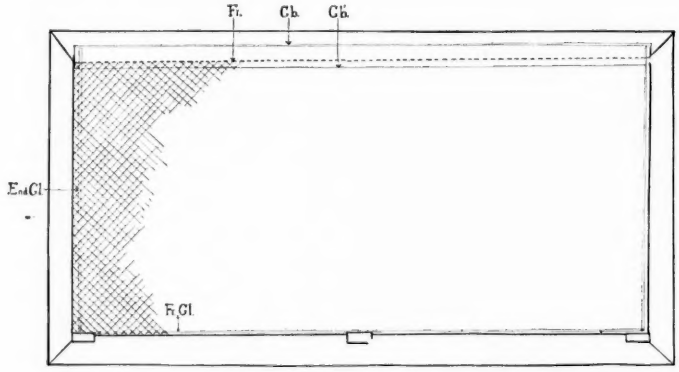

FIG. 4. BOTTOM VIEW OF THE CASE. The wire mesh is partly drawn in to show its relation to the end (*End. gl.*) and front glass (*Fr. gl.*), and to the galvanized iron back (*Gb'*). *Fr.*, frame.

From a sanitary point of view too much emphasis can hardly be placed upon the construction of the bottom. By using ¼ inch wire mesh through which waste material will readily fall, I have succeeded in providing a case which in a large measure is self cleaning. The cases thus constructed are placed on a long trough-like table, cov-

ered with galvanized iron, which drains into a sink. By flushing off the top at intervals, the waste is easily disposed of.

While the use of glass in case building may imply an increase in the cost of construction, yet in the above plan it is believed that this cost has been reduced to a minimum, and that a case has been provided which in addition to its quality for observation assures unusual conditions of sanitation.

A point of great importance in the construction of such a case is that the galvanized iron back and the side and front glasses rest on the mesh-bottom so that waste material in falling through does *not* strike the framework of the case. It will be seen from a view of the bottom (Fig. 4) that the back of the case is bent inward an inch from its base so as to come well out on the mesh bottom, and that the sides and front are placed well over the line of the framework of the bottom.

2. *Nest Boxes and Nesting Materials.*—I have followed with satisfactory results the largely used plan of having a winter and a summer nest box. The winter nest box is made by cutting a chalk box to three-fourths size. This is filled two-thirds full of nesting material. The summer nest is a small sized box similarly furnished.

Various materials have been tested for nesting, to many of which objections can be made. Cotton although warm, retains odor and at the same time offers a more serious objection in that the young often become entangled in it, and are thus permanently injured or even killed. Excelsior I have found to make a good nest if lined with some sort of soft material, as, for example, crude floss. One of the most satisfactory materials which I have tried for nesting is the shredded paper used in the packing of china. If this can not be procured at the china store it may be prepared by cutting up any kind of soft paper.

3. *Food Receptacles and Food.*—I have tried various kinds of food receptacles, most of which have given little or no satisfaction. The difficulty of keeping the food reasonably clean in open food cans is so great that some

sort of device for its protection is essential. The plan that I have found most successful has been to place bird cups in the nest box so that the mouse can procure the food through an opening in the front of the box. The cups are further provided with an apperture in the top through which, without opening the case, food may be added. This method of feeding, by preventing the mouse from running over the food, holds in abeyance the spread of disease.

The most satisfactory food that I have used for mice is wheat, added to which is a small amount of stale bread. These, together with milk—which is given by a modification of the method below described for water—constitute the daily and constant diet. Occasionally sunflower seed and a few leaves of lettuce may well be given for a change.

4. *Water Receptacles.*—The inverted bottle which is now in general use for supplying water has done much to eradicate ills resulting from a bad water supply. By this device a large quantity of water can be provided which is a great advantage in general cultures. In many kinds of experiments, however, it is desirable to keep water in greater purity than is possible even by this method. To do this I have found a device which is strikingly simple and at the same time singularly effective in that it keeps the water in contact only with glass. My plan consists in closing the end of a specimen-tube (or test-tube) in a frame so that the opening is just large enough to retain the water drop when the tube is filled and inverted in the case.[3] These inverted tubes are inserted through holes made in the top of the case and are prevented from falling through by means of small rubber bands placed around the closed ends of the tubes. The tube may then be removed and refilled without opening the case, the refilling being done from a siphon bottle.

The addition of these devices for food and water to a mesh-bottom case I have found to aid much in the inten-

[3] The tube for milk, instead of having one end closed permanently as in the test-tube, has the end closed with a rubber stopper, the advantage of this being the ease with which such an open tube upon removal of the stopper can be cleaned.

sive breeding of mice. But to rear mice successfully further requires a practical knowledge of their breeding habits.

III. Breeding Habits of Mice

Copulation in mice is a well-defined act which usually follows only upon the persistent efforts of the male. It is marked by a period of union which lasts for several seconds (ten to twenty-five) and is followed by an interval of more or less complete rest.

Practical questions for the breeder are: 1. When will copulation occur—that is, when is the period of heat? 2. What is the duration of this period? 3. How often does the period of heat recur? To the last of these questions my experience can offer no answer; and to the second my observations add little. In one case, however, after a double copulation had been observed in the evening copulation again took place on the following morning. The fact that the beginning of heat is shown in some as early as five hours after parturition and is delayed in others as long as thirty-six hours thereafter makes it difficult to determine with exactness the duration of this period.

As to the first question—When may copulation be secured?—two periods can be determined with considerable accuracy. One of these closely succeeds parturition, the other follows upon a period of rest.

In the first case, if the female has given birth to young, copulation will usually take place, if she is put with the male, within from five to twenty-four hours.[4] In my own experience I have found that the greater number of births take place in the early morning, and that copulation will, in such a case, occur from seven to eight o'clock in the evening. The female is not invariably in heat at this time, however, as has been shown by a considerable number of cases which I have observed.

The second period in which copulation may be expected is after a mother has gone through an interval of rest,

[4] This is seen to correspond roughly to the time of ovulation in mice, as shown by Long (5), the period given being from 14½ to 28½ hours after parturition.

either after having suckled her young or after having lost them. She will then ordinarily copulate within a few days after having been put with the male. The following representative table of ten consecutive cases emphasizes this point.

TABLE I

Example	Put with Male	Young Born	Interval Elapsing, Days
1	April 2	April 25	23
2	April 5	April 26	21
3	April 12	May 4	22
4	April 19	May 11	22
5	April 29	May 21	22
6	May 14	June 6	23
7	May 18	June 11	24
8	May 26	June 24	29
9	May 27	June 18	22
10	June 11	July 3	22

Out of the above ten cases in which the females had not suckled young for some time, and then were put with males, nine cases of copulation evidently resulted early, since the young were born within an interval only a little greater than the normal period of gestation following a rest (that is, 20 days) (6).

The eighth case, although unusual, has been further accentuated by more recent data which show that the female may remain with the male for long periods without becoming pregnant. This is not conclusive evidence, however, that an unsuccessful copulation may not have taken place within that time. In fact, I have found that in a surprising number of cases copulation does not result in fertility. As an example of this may be cited 25 consecutive cases which I observed, 10, or 36 per cent., of which resulted in infertilty.

In interpreting this sterility I was at first inclined to believe that it was due entirely to the females, but since then I have found males in many cases unproductive. Some of these were useless for breeding because they were practically unresponsive, rarely if ever copulating; others, although among the most active males, proved unfertile. The following example may be given to show such a case.

TABLE II*a*

RECORD OF ♂ No. 6

No. of ♀	6	9	2	5	6	4	2	1	14	10
Date of copulation	12/3	12/7	12/8	12/14	12/23	12/27	12/30	1/6	4/3	4/19
Result	Fert.	Infer.	Fert.	Fert.	Infer.	Fert.	Infer.	Infer.	Infer.	Infer.

In the above table is given the record of one of the most active males that I have yet had. The record, however, shows that, although mated with vigorous females, only 40 per cent. of the copulations resulted in offspring. The table further shows that after a rest from January to April infertility is still shown. At this later period the male had become inactive, so that it was difficult to secure a copulation.

A relatively high index of fertility is shown in the record of a male designated as No. 5.

TABLE II*b*

RECORD OF ♂ No. 5

No. of ♀	3	4	3	5[5]	3	4	9	6	1	2
Date of copulation.	12/3	12/7	12/28	1/3	1/17	1/21	3/8	3/13	3/13	4/6
Result	Fert.	Fert.	Fert.	Infer.	Infer.	Fert.	Fert.	Fert.	Fert.	Fert.

Number 5 when mated with females equally as active as those with which No. 6 was mated gave 80 per cent. of fertility. Within this series were also two other copulations by the same mouse, but since these were with female No. 4, which always proved fertile, they were eliminated and only those counted which were entirely comparable with those of No. 6.

It may be said that both males and females are found which have a low index of fertility. Intensive breeding requires that these be eliminated and that those be selected the copulations of which result in a high percentage of fertility.

When fertility does result from a copulation, the ensuing period is of singular interest to the investigator. This I have discussed in a former paper[6] in which I have

[5] Seriously ill after the birth of her young.

[6] Loc. cit.

shown that the period of gestation depends upon the state of the female. If the pregnant female is not suckling young, parturition with but rare exceptions takes place on the twentieth day after copulation. If she is suckling on the other hand, the period varies with the number of young suckled. Thus, for example, if the mother be suckling five during gestation she may be expected to go about twenty-five days; if ten thirty days.

Parturition, which terminates the period of gestation is normally of brief duration, even in case a large litter is born. But this is not invariable, for I have observed cases in which labor was prolonged, and some in which unaided birth was impossible.

We are inclined to believe that in mankind the difficulty of giving birth, which not infrequently results in the death of the mother, is due to the artificialities of civilized life. But here we find the same stern fact emphasized in a type remotely removed from any such influence.

IV. Rearing of the Young

The most hazardous time in the life of a mouse is the first few days of its existence. Born helpless and naked it is dependent upon the mother not alone for nourishment but for warmth as well. Some mothers at this time are most solicitous for their young, building elaborate nests for them and giving such care to the young as to tide them over this early period. Others there are that not only withhold the requisite care, but which at this time prove the most serious menace. Some of these bundle their young away in the nesting to die; while others in bad conditions openly destroy them. This singular and, so far as I am aware, unexplained phenomenon of destroying the offspring, is carried to a high pitch in the case of mice. Under unfavorable conditions of temperature, nesting and the like, I have seen three or four litters destroyed in succession. Miller (7) in a study of the brown rat shows that this destructiveness in the rat is carried to even a greater extent than in the case of the mouse.

If the young escape the perils of the first few days they usually grow rapidly and, at the end of a few months, reach maturity. There is a disease, however, which at the end of the second week may attack the young, leaving them emaciated or, when more severe, killing them in great numbers.

Between birth and maturity four well-defined stages occur. To know these is often of practical service to the breeder for the determination of age, sex and the like.

The first stage is that in which the newly-born young have a peculiarly red and transparent skin through which is seen the stomach white with milk. Following this at the end of the sixth or seventh day a *second stage* is evident in which the body is covered with flaky scales of dandruff—the forerunners of a coat of silky fur. *A third important stage,* which I have designated as the early stage for distinguishing sex[7] is usually shown on the ninth or tenth day, at which time the mammæ in the young females appear. These can be observed for an interval up to the thirteenth or fourteenth day, at which time the fur usually obscures them.

Determination of sex after the body is covered with fur, for example at the time of weaning, is often difficult. Because of this I have found it advantageous at the end of the third period to mark the young females by clipping a tuft of fur at the root of the tail, so that later, when they are to be mated, no difficulty is found in distinguishing with certainty males from females.

The fourth period, on the fourteenth day, is characterized by the advent of sight. This like all other periods shows slight variation. While in a few cases I have found the eyes to open as early as the thirteenth day, in others, equally normal in other respects, I have found them to be delayed until the fifteenth and even the sixteenth day. The regularity with which this period occurs, however, is a sufficiently exact criterion to make it an index of age.

From the fourteenth day to the twenty-first, the date

[7] This does not mean that sex can not be determined earlier than this period. As a matter of fact, sex can be determined at birth, this, however, is difficult and less certain than to determine it at the third period.

at which the young should be weaned, no definite change, except increase in size, is shown.

With the period of sexual maturity we may count the cycle of development complete. This does not imply, however, that growth ceases at this time. The time at which mice reach sexual maturity varies greatly. While I have had some mice to pair at six weeks, this is rather unusual. It has been my experience that under ordinary circumstances both the males and females reach sexual maturity in the second or third month. From this time on for the next few months the mice are in the prime of the reproductive period, beyond which, at the end of ten to twelve months of age, activity diminishes and, for purposes of breeding, the mouse is of little further service.

V. PRACTICAL SUMMARY

The ease with which white mice can be handled makes them in many cases preferable for experimentation to other and larger rodents, but their usefulness has been greatly curtailed because of a wide-spread notion that they are difficult to rear under the conditions of the laboratory.

The purpose of this paper is to give an intensive method by which I have been able to rear then in abundance. By "intensive" I mean that relatively few mice are kept from which to breed, and that these are kept under conditions which insure productivity.

Especially detrimental to intensive breeding are parasitism and marked fluctuations in temperature. Hot air heat, the temperature ranging from 20° to 25° C., has proved most satisfactory. Heat from an oil stove when continued for a considerable length of time proved unsatisfactory.

Mice which are badly parasitized are useless for breeding purposes. Various kinds of sprays and powders are used to rid them of the parasites. Some of these, however, I have used with disastrous results. Parasitism may be best prevented by using a case that is readily cleaned. My cases are washed weekly with hot water to

which is added "gold-dust" and a small amount of petroleum; the nest-boxes, into which the mice are put at the time of cleaning, are partly closed and then removed from the case.

Essential to intensive breeding is an adequately equipped case. A most essential requisite is a wire mesh bottom through which waste material readily falls. If such a case be placed on a table with a trough-top lined with galvanized iron, waste matter can easily be drained into a sink. For nests the case is provided with three-fourth sized chalk boxes filled two-thirds full of shredded paper. Food (wheat) is procured by the mice through an opening in the front of the nest box from bird cups placed inside of the box. These are filled from the outside without opening the case. Water may be kept in excellent condition in test-tubes which are closed sufficiently to retain the water drop when the tube is inverted in the case; these are filled from a siphon bottle.

A knowledge of breeding habits is of great importance in intensive breeeding. Copulation in mice is a well-defined act, which lasts from ten to twenty-five seconds and is followed by a more or less complete rest. It normally takes place on the day that a litter is born. In females that have gone through a period of rest it will usually occur a few days after the female has been put with the male. Copulation may or may not result in fertility. By a selection of males and females with a high index of fertility the number of offspring may be greatly increased.

The period which a non-suckling mother carries her young is a few hours short of twenty days. A mother suckling young, on the other hand, carries her litter twenty plus the number that she is suckling. Thus a mother suckling five will go practically (20 +5) twenty-five days, while one suckling ten may be expected to run (20+10) thirty days.

In rearing the young it is well to remember that the greatest mortality results within the first two or three days of life. At this time the young must be kept warm. Under bad conditions the mother may destroy them.

From birth to maturity mice pass through several well-defined stages which to the breeder are of importance for the determination of age, sex and the like. These are 1 an early stage in which the skin is peculiarly red so that through it may be seen the stomach white with milk; 2 a second stage at six to seven days in which the body is covered with flakes of dandruff; 3 a stage at nine or ten days in which the mammæ appear in the females. This I have designated as the stage for the early determination of sex; 4 on the fourteenth day a stage at which the eyes open.

At twenty-one days the young should be weaned. From this time on slight change is shown except increase in size until sexual maturity is reached. This usually occurs in the second or third month. From this time up to the end of ten months or a year of age the mouse is in the height of the breeding period; beyond this time, for purposes of breeding, the mouse is usually of little further service.

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THE DISTRIBUTION OF HYLA ARENICOLOR COPE, WITH NOTES ON ITS HABITS AND VARIATION

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STUDENTS of zoogeographical distribution are frequently hindered by the scarcity and inexactness of the published data in the particular group which they are studying. Especially is this true of students of western North American amphibians, for they must rely largely upon the publications of the early exploring expeditions in which localities were often stated in a most general way and at times with doubtful accuracy.

Our present knowledge of the distribution of the tree toad, *Hyla arenicolor* Cope, is very incomplete. Many of the references to its occurrence are extremely indefinite and unreliable and in no case has enough material been gathered to give the limits of its range in any one region. It was first discovered and named *Hyla affinis* by Baird[1] in 1854, the description being based upon one specimen from the state of Sonora, Mexico. Later Cope[2] found this name to be preoccupied and replaced it with *arenicolor*. At the present writing this tree toad is known to inhabit parts of southern California, Utah, Arizona, New Mexico, Texas, and Mexico. Southern California is included in its range on the strength of two specimens collected in 1875 by H. W. Henshaw,[3] and no additional records of its occurrence within the state have been made by the herpetologists who have explored this region. Within the last few years, however, the University of California Museum of Vertebrate Zoology has acquired a number of specimens of *Hyla arenicolor* from various

[1] *Proc. Acad. Nat. Sci. Phila.*, p. 61.

[2] *Journal Acad. Nat. Sci. Phila.*, 1866, p. 84.

[3] Yarrow, *Bull. U. S. Nat. Mus.*, No. 24, 1882, pp. 24, 175.

localities in southern California. Through the kindness of the director, Professor J. Grinnell, the writer has been extended the privilege of examining these specimens and the results are incorporated in the present article. Specimens from the following localities have been studied, all of which are in the Museum of Vertebrate Zoology unless otherwise stated.

TABLE A

No. of Specimens	Locality	Altitude	Date	Collector
8	Mountain Spring, San Diego Co., Cal.	About 4,500 ft.	1909 Mar. 25	F. Stephens
1	La Puerta, San Diego Co., Cal.	About 4,500 ft.	June 5	F. Stephens
1	Warner's Pass, San Diego Co., Cal.	4,000 ft.	June 22	F. Stephens
1	Julian, San Diego Co., Cal.	3,750 ft.	July 29 1906	F. Stephens
3	Pine Mt., near Escondido, Cal.	2,750 ft.	Sept. 4 1908	J. Dixon
1	Carrizo Creek, Santa Rosa Mts., Cal.	3,000 ft.	June 22	J. Grinnell
2	Dos Palmos Springs, Santa Rosa Mts., Cal.	3,500 ft.	May 26	J. Grinnell
9	Deep Canyon, Santa Rosa Mts., Cal.	3,000 ft.	June 21	J. Grinnell
1	Lower Palm Canyon, San Jacinto Mts., Cal.	800 ft.	June 15	J. Grinnell
2	Oak Springs, upper Palm Canyon, San Jacinto Mts., Cal.	4,750 ft.	June 11	J. Grinnell
4	Base of San Jacinto Mts. near Cabazon, Riverside Co., Cal.	1,700 ft.	May 5 and 7	W. P. Taylor and C. H. Richardson Jr.
4	Sierra Madre, Los Angeles Co., Cal.	1,500 ft.	May, 1904 1903	J. Grinnell
20	Arroyo Seco Canyon near Pasadena, Cal.	1,500 to 2,000 ft.	Aug. 3 and 23	J. Grinnell
1	Tejunga Valley, Los Angeles Co., Cal.	About 1,500 ft.	1910 Apr. 1	J. Grinnell
1	(Stanford University coll.) Upper Santa Anita Canyon, Los Angeles Co., Cal.	3,500 ft.	Aug. 7	C. H. Richardson, Jr.

In California, *Hyla arenicolor* is now known to range northward along the coast mountains from near the Mexican boundary to the Tejunga Valley, Los Angeles County. In San Diego County it occurs on both the coast and desert slopes of the mountains; in Riverside County, on the desert slope, and in Los Angeles County, so far as known, only on the coast slope. No records of its

occurrence in San Bernardino County are at hand, but a careful search will undoubtedly reveal its presence there. Throughout this region, its habitat appears to be confined to streams and mountain springs between 1,000 and 5,000 feet elevation. Here the writer has found it associated with such trees as *Alnus rhombifolia, Platanus racemosa,* and *Acer macrophyllum* and in this state at least it may be regarded as an inhabitant of canyons within the upper sonoran zone. It is apparently more strictly aquatic than the smaller *Hyla regilla* Baird and Girard, whose range in southern California is, in part, coextensive with it. The former species has never been found far away from the vicinity of water, while the latter has often been seen under vegetation a considerable distance from it.

The following meager notes indicate that the breeding season of *Hyla arenicolor* extends from late spring until fall: Two females from Sierra Madre, Los Angeles County, May, 1904, one from Warner's Pass, San Diego County, June 22, 1909, and one from Pine Mountain, near Escondido, San Diego County, Sept. 4, 1906, contain large eggs. There is also a young specimen from La Puerta, San Diego County, collected on June 5, 1909, in which the tail has not been entirely absorbed.

Miss Dickerson[4] has described the rapid color changes that take place in this species. The writer noted that a light-colored individual which was captured on a granite rock changed to a dark gray mottled with lighter markings when placed for a short time in a covered tin pail.

The widely scattered record stations given below, some of which are too inexact to be of great value, suggest that *Hyla arenicolor* lives in suitable places over practically the entire southwestern part of the United States and a considerable portion of the Mexican tableland as well. Little has been written concerning its habitat preferences within this region. Stejneger[5] has found it in the Grand

[4] The Frog Book, Doubleday, Page and Company, 1906, p. 122.
[5] N. A. Fauna, No. 3, 1890, p. 117.

Canyon of the Colorado, Arizona, at an elevation of 1,000 feet above the river and in the bottom of the canyon. Ruthven's[6] specimens from Sabino Canyon, Santa Catalina Mountains, Arizona, were "found among bushes on the floor of the canyon" in the "willow-poplar association."

TABLE B

No. of Specimens	Locality	Date	Authority
1 type	Sonora, Mexico	.....	Cope; Baird
	Guanajuato, Mexico	.....	Duges
	Guadalajara, Mexico	.....	Duges
	Between City of Mexico and Chihuahua, Mex.	.....	Cope
	Valleys of Mexico or Toluca Mexico	.....	Cope
1	Del Rio, Texas	.....	Witmer Stone
2	El Paso, Texas	.....	Boulenger
1	Santa Fe, New Mexico	June, 1873	Yarrow
1	Fort Wingate, New Mexico	.....	Cope
1	Utah	1872	Yarrow
	Tucson, Arizona	.....	Miss Dickerson
	Upper Colorado River	.....	Cope
	White River Canyon, Arizona	.....	Cope
6	Grand Canyon of the Colorado, Arizona	Sept. 3, 1889	Stejneger
	Fort Whipple, Arizona	.....	Cope
2	Sabino Canyon, Santa Catalina Mts., Ariz.	May 23, 1903	Ruthven
2	Southern California	1875	Yarrow

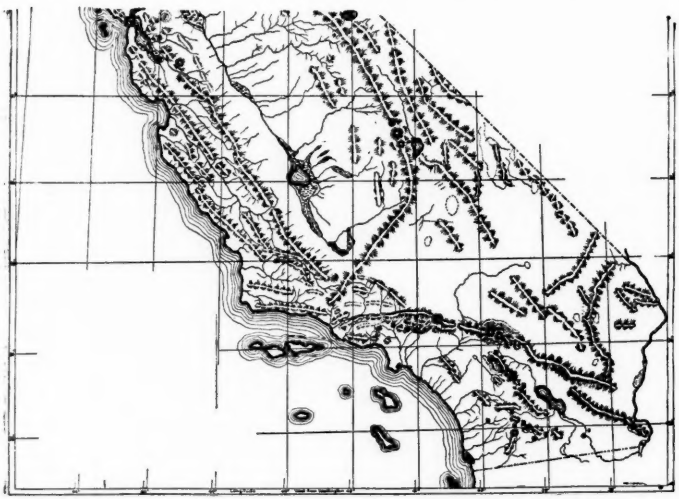
Specimens of *Hyla arenicolor* from southern California agree quite closely with the published descriptions. Cope[7] states that the diameter of the tympanum is equal to two thirds that of the eye fissure, but in ten specimens measured (see following table) this ratio is shown to be 47.7 per cent., or not quite one half. Boulenger's *Hyla copii*[8] described from two specimens obtained at El Paso, Texas, and now considered synonymous with *Hyla arenicolor,* has the diameter of the tympanum one half that of the eye fissure, a fact which suggests that this character is subject to considerable variation throughout the range of the species. The ratio between the length of the body and that of the hind limb is also subject to

[6] *Bull. Am. Mus. Nat. Hist.*, 1907, p. 509.
[7] *Bull. U. S. Nat. Mus.*, 1889, No. 34, pp. 369–370.
[8] *Annals and Magazine Nat. Hist.*, 1887, p. 53.

TABLE OF MEASUREMENTS (IN MILLIMETERS)

No. (U. C. M. V. Z.)	Sex.	Length Snout to Anus	Width Head at Posterior Angle of Eye	Fore Limb	Hind Limb from Tip of Urostyle	Tibia	Diameter of Tympanum	Diam. of Eye	Ratio Diam. of Tympanum to Diam. of Eye	Locality
920	♂	35.5	12.5	22.3	57.5	20.	2.5	4.	.625	Sierra Madre, Los Angeles Co., Cal.
977	♂	33.	12.	20.	53.5	18.	1.5	4.	.375	Mountain Spring, San Diego Co., Cal.
979	♂	34.9	13.	19.3	53.	18.	2.2	4.	.55	Mountain Spring, San Diego Co., Cal.
980	♂	33.3	13.2	18.5	50.3	16.5	1.8	4.4	.409	Mountain Spring, San Diego Co., Cal.
976	♂	30.	11.1	18.2	50.	17.	1.6	4.	.40	Mountain Spring, San Diego Co., Cal.
978	♂	33.8	12.6	21.5	55.	18.	2.	4.5	.444	Mountain Spring, San Diego Co., Cal.
922	♀	40.	16.	26.	67.	22.	3.	5.	.60	Sierra Madre, Los Angeles Co., Cal.
921	♀	38.	13.	23.	63.	21.	2.	4.	.50	Sierra Madre, Los Angeles Co., Cal.
929	♀	37.	13.8	23.5	67.	21.5	2.	4.5	.444	Pine Mountain, near Escondido, San Diego Co., Cal.
1037	♀	40.2	15.	25.	70.	22.	2.	4.7	.425	Warner's Pass, San Diego Co., Cal.

pronounced variation in southern California specimens. The heel of the limb when extended forward usually reaches to the anterior border of the orbit,[9] but in young individuals it often extends to the tip of the snout.



THE DISTRIBUTION OF *Hyla arenicolor* COPE IN CALIFORNIA ACCORDING TO THE LOCALITY RECORDS.

The table also shows that there is a well-marked difference in the size of the sexes, the female being larger, especially in the length of the body and hind limbs.

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[9] Cope, *loc. cit.*

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THE UNEXPECTED OCCURRENCE OF ALEURONE COLORS IN F_2 OF A CROSS BETWEEN NON-COLORED VARIETIES OF MAIZE

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BEFORE the Mendelian methods of analysis became available, considerable wonder would doubtless have been excited by the "mysterious" appearance in F_2 of one colored grain—purple or red—to every five or six white ones in case of a maize cross, both parents and F_1 of which had only white grains. An occurrence of this sort has recently been noted in one of my maize cultures and the F_2 numbers are explained here as a trihybrid or tetrahybrid ratio. The crosses in question were made primarily for a study of size inheritance and fairly large numbers have been grown. The varieties concerned are two dwarfs of distinctly different types, Tom Thumb pop and California Rice pop, and a tall type Missouri dent. The facts with reference to aleurone color are these: Tom Thumb pop, a "white" corn (*i. e.*, having non-colored aleurone), was crossed with Missouri dent, also a white corn. Three generations of hybrid plants—four generations for aleurone and other endosperm characters—have been grown without the appearance of any but white grains. The same white-seeded Missouri dent was also crossed with the white-seeded California pop. The three hybrid generations grown to date have shown no aleurone color. Furthermore, when the same white Tom Thumb pop was crossed with the same white California pop, only white grains appeared in F_1. But both of the two ears containing F_2 seeds—the only ones that have been produced as yet—had a sprinkling of both purple and red grains, too many to be explained as due to care-

less guarding against foreign pollen and too few to be accounted for by any simple monohybrid or dihybrid formula. The actual numbers of grains of the various sorts were as follows:

Ear 1	43 purple,	10 red,	308 white.
Ear 2	32 purple,	11 red,	222 white.
Total	$\overline{75}$ purple,	$\overline{21}$ red,	$\overline{530}$ white.

The fact is familiar that in crosses of purple with white varieties of corn, there often appear in addition to the monohybrid ratio of three purple grains to one white one, purple, red and white grains in the dihybrid ratios of 9:3:4 (East and Hayes[1] and Emerson[2]). It is also well known that in similar crosses purple and white grains may appear in F_2 in the reversed monohybrid ratio of 1:3 or the dihybrid ratio of 9:7 (East and Hayes[1]). East[3] has recently shown that for the production of purple aleurone there must be present three Mendelian factors, *C*, *R*, and *P*, and has demonstrated for purple, red, and white grains the trihybrid ratio of 27:9:28. *C* is a general color factor, that must be present ordinarily in order that any color may develop, *R* a factor that has to do with the production of red aleurone when *C* is present, and *P* a factor for purple that is effective only in the presence of both *C* and *R*. Thus *CRP* gives purple and *CRp* red, while all the other possible combinations give white. All this is on the assumption that a fourth factor *I*, an inhibitor of color development, is absent. Purple color of the aleurone may, therefore, be said to depend upon the presence of three factors and the absence of one, *CRPi*, red color upon the presence of two factors and the absence of the two others, *CRpi*, and whites upon the absence of either one of the two factors *C* or *R* or upon the presence of a third factor, *I*, *cRP*, *CrP*, or *CRPI*, etc.

[1] E. M. East and H. K. Hayes, Conn. Agr. Expt. Sta., Bul. 167, pp. 57–100, 1911.

[2] R. A. Emerson, Amer. Breeders' Assoc., vol. 6, pp. 233–237, 1911.

[3] E. M. East, AMER. NAT., vol. 46, pp. 363–365, 1912.

If the numbers obtained in F_2 of the cross of Tom Thumb pop with California pop are to be regarded as constituting a tetrahybrid ratio, all four aleurone factors must be heterozygous in F_1 the formula being *CcRrPpIi*. The F_2 generation would then be constituted as follows:

27 *CRPi*	.....	27 purple
9 *CRpi*	.....	9 red
9 *CrPi*		
9 *cRPi*		
3 *Crpi*		
3 *cRpi*		
3 *crPi*		
1 *crpi*		
81 *CRPI*		
27 *CRpI*	.....	220 white
27 *CrPI*		
27 *cRPI*		
9 *CrpI*		
9 *cRpI*		
9 *crPI*		
3 *crpI*		

If either *C* or *R* is homozygous in F_1, the resulting F_2 ratio should approximate 9 purple: 3 red: 52 white.

The actual numbers fell between these two theoretical ratios, as is seen from the following comparison:

	Purple	Red	White	Total
Tetrahybrid ratio	66	22	538	626
Observed numbers	75	21	530	626
Trihybrid ratio	88	29	509	626

From the ratio alone it is plainly impossible to say whether the cross in question is a tetrahybrid or a trihybrid. Of course behavior of the reds and purples in F_3 will settle the matter. If, for instance, either *C* or *R* is homozygous, one third of the F_2 red grains should breed true and two thirds produce reds and whites in the ratio of 3:1, while if both are heterozygous, only one ninth of

them should breed true, four ninths produce a 3:1 ratio, and four ninths produce a 9:7 ratio. Similarly, if either one of these two factors is homozygous, of the F_2 purples one ninth should breed true, two ninths give purple and red 3:1, two ninths purple and white 3:1, and four ninths purple, red, and white 9:3:4. But if both factors are heterozygous, out of the twenty-seven F_2 purples only one should breed true; two yield purple and red 3:1; four, purple and white 3:1; four, purple and white 9:7; eight, purple, red and white 9:3:4; and eight, purple, red and white 27:9:28.

The results of intercrossing Tom Thumb pop, Missouri dent and California pop, so far as they are known at present, might be obtained if the three varieties had either of the following sets of formulæ, or any of the modifications of them suggested below:

Tom Thumb pop	*ICRP*		*ICrP*
Missouri dent	*IcRP*	or	*icrP*
California pop	*icrp*		*icRp*

Among the allowable modifications of the above formulæ are these: The formulæ for Tom Thumb pop and California pop may be interchanged. Substitutions of *C* for *R* and *R* for *C* may be made if carried throughout the set. *P* may be present in any one or two varieties and absent from any one or two. Where *I* is present in Missouri dent and also in one of the other varieties, *R* may be present in all three varieties, absent in any one variety, or absent in Missouri dent and either one of the other varieties.

A NEW SUBSPECIES OF ZEA MAYS L.

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WHILE harvesting a plot of yellow dent corn, a strain of the Leaming variety grown on the Illinois Agricultural Experiment Station fields in 1909, one of the workmen found a peculiarly shaped ear which was laid aside in the drying-room as a curiosity. The corn in which this ear was found came from a strain that had been subjected for several generations to an ear-row selection for high protein content by a mechanical inspection of the endosperm.[1]

This new type of ear which reproduces faithfully in its progeny is cone-shaped in outline and gives the appearance externally of being composed of a mass of kernels borne on numerous irregular branches (see *"a"* in the figure). A longitudinal section (at *"b"*) displayed kernels throughout the ear.

The "branched" form is a prolification of the fleshy type of 4 to 30 or more-rowed cob common to all varieties that to the writer's knowledge have been described to date. For this new type the writer proposes the name *Zea ramosa,* from the Latin *"ramosus*—having many branches." This name is proposed in conformity with the bi-nomial classification of Sturtevant[2] which is now generally recognized. We will not here discuss the precedence nor the desirability of Sturtevant's nomenclature for the subspecies of corn which were all grouped at first by Linnæus under the general head *Zea mays.*

The new type *Z. ramosa* (branched) is as much deserving of a specific name as are any of the six groups recognized by Sturtevant, namely: *tunicata* (pod), *everta* (pop), *indurata* (flint), *indentata* (dent), *amylacea* (soft), *saccharata* (sweet). The first of these six groups has a more or less monstrous development of glumes into pods which inclose each kernel on the ear with leafy bracts known as the husks. The classification of the other five groups is based on differences in characters situated in the endosperm of the kernel.

[1] Representative samples of the ears thus obtained for planting in the next year were also analyzed chemically to determine the efficiency of the method of mechanical selection.

[2] Sturtevant, E. L., *Bul. Torr. Bot. Club,* 21: 319–343, 1894; Off. Exp. Sta. U. S. D. A., Bul. 57: 7–108, 1899.

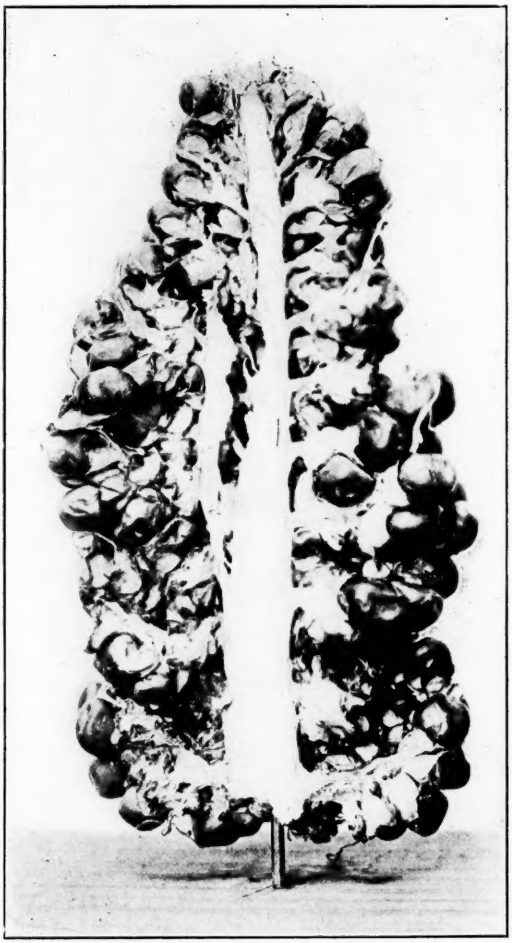
The ear of *Z. ramosa*, which is always of a definite form, is borne at the usual place near the middle of the culm and is not to be confused with sparsely branched ears sometimes found on the culm nor with ears frequently found in the tassels on ordi-

a

THE NEW TYPE OF EAR AND TASSEL IN CORN (*Zea ramosa*). *a*, external view of parent ear. *b*, longitudinal section of same (p. 619). *c*, tassel (p. 620). Photographs by Flora Sims and by courtesy of the Illinois Agricultural Experiment Station.

nary corn plants. Such abnormalities which are fluctuating in their inheritance have thick basal branches of fleshy cob—which may be as long or longer than the primary cob itself—and may bear from two to a dozen or more rows of kernels on each branch. Furthermore, no male florets have as yet been found in any of the ears of *Z. ramosa* and they are always covered with normal husks.

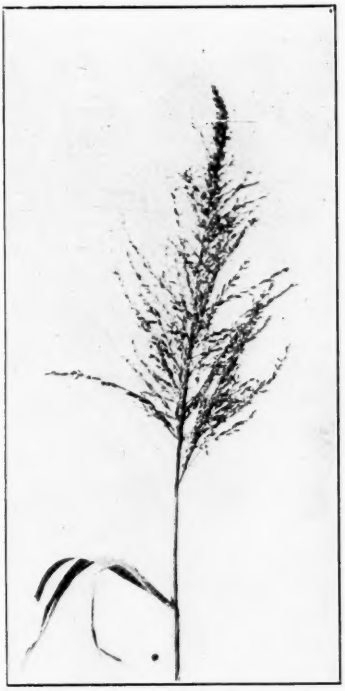
A feature of especial interest in the new type is the fact that the tassels of such plants are also invariably much branched and



b

cone-shaped. (A reduced photograph of the tassel is shown at "*c*.") No instance has yet appeared in which this correlation did not exist.

During the last three years the writer has had under observation a large number of varieties and their hybrids. He has been able to isolate more than a dozen tassel types which are strikingly different in shape and which are distinct from each other in inheritance. Some of the characters of these types are plainly correlated with certain characters of the ear. Advantage can undoubtedly be taken of this fact in analyzing the behavior of such fluctuating phenomena as size, shape, and number of parts.



c

This correlation between tassel and ear permits the selection of individuals in the field before the silks appear. These plants may then be bagged and hand pollenated at will. In an investigation not yet published, the writer has found that the tassels in a large number of varieties are usually out and fully expanded one or more days before any pollen is shed from the anthers, while the tassels produce pollen at an average of from one to three days before the silks appear on the same plants.

During the first season (1910) in which the branched ear was tested to see if it would reproduce the character only two out of fifty kernels planted produced individuals bearing the branched ears. It was at this time that the correlation between the tassel and ear type was discovered. The fact that only two plants of the *Z. ramosa* type were obtained this first year indicated that either the character was reproduced only occasionally or that it was a recessive character and that the parent was pollenated largely by neighboring plants bearing normal ears which must be dominant to the branched form. It was pre-

dicted[3] that the latter explanation was the true one, and the results from another generation (grown in 1911 from hand pollenated ears) have substantiated the prediction. Our data for this year show that the branched form of ear and its accompanying tassel type are recessive to the fasciated, cylindrical form of ear from which they originated.

Perhaps no one is ready to draw the limits upon that indefinable term "species," but Mendelian studies have thrown a bright light upon this mooted question. It is now very evident that sterility in hybrids is not a safe guide for determining what shall be a species. Darwin reported a number of cases to show the fallacy of this theory which was at one time advanced by Kölreuter, Gärtner and others. Mendelian studies have disclosed a number of cases of sterility (I have found several in corn) which are not due to hybridization nor to species' differences.

Systematic classification should be founded upon either the genotype or upon the Mendelian basis. The genotype basis would be feasible for self-bred and apogamous, including parthenogenetic, types of reproduction; while the Mendelian basis would undoubtedly be the most satisfactory for types of plants and animals that are continually mix-fecundated. We are learning that there are an almost inestimable number of characters in corn and that they may be quickly distributed to all the representatives of the six species-groups by hybridization. As an example: the kernel colors; red, yellow, blue and their absence (white) are found in all of the groups. If we were to give each distinct character, wherever we find it, a specific classification we should have many more species than we now recognize. This is especially true with regard to economic plants.

Such classification is desirable, however, and will soon be needed from a Mendelian standpoint if from no other. As an instance: we have evidence that there are more than twenty reds or phases of red color in corn alone, and a system for their classification is desirable. As was mentioned above, we have isolated a dozen distinct tassel types, each possessing a number of characters that may be easily redistributed by hybridization. The inheritance of detail in both plants and animals is various:

[3] "The Analysis of Characters in Corn and Their Behavior on Transmission," a paper submitted May 13, 1911, to the graduate school of the University of Illinois as a doctorate thesis.

when true dwarfs and true giants are hybridized, size segregates distinctly in their progeny; but when fluctuating shorts and talls are hybridized, size exhibits a so-called "blending" behavior that is generally complex. Thus it is evident that for recording such characters and their method of segregation we already need for the sake of conformity, brevity and ease in reference *a definite, simple, systematic classification of characters irrespective of species, varieties or individuals.* Bateson, by grouping characters of similarity under one head; Tschermak and others, by distinguishing "types" of segregation, have already taken a step toward this end.

The newly discovered type of corn is so radically different from all others yet reported, and since we are at present recognizing six species-groups of *Zea,* it seems very appropriate to add *Z. ramosa* as a seventh. And yet the writer will not be disappointed if the proposed addition is not recognized.

That *Z. tunicata* and *Z. ramosa* both originated as mutations we have no doubt; but as to the causes which led to the production of these two peculiar types, we have no definite knowledge. It has been proposed that new forms, aside from those developed by hybridization, are due to accidents in mytotic division; and yet those same writers are perhaps not ready to admit that even the greater proportion of the myriads of diverse forms of plant and animal life that exist on the earth to-day are accidents! This, of course, has nothing to do with the fact of chance meeting of gametes in reproduction.

The writer has evidence (not yet published) upon various strains of pod varieties and their hybrids with other podless varieties to show that the pod character, in that form, never was the normal or original pod or glume in *Zea;* and it is also evident that the new branched ear, as it is, is not a reversion to a former one. As may be seen at *"b"* in the illustration, the pithy core of the cob is not affected by the branching in the outer zone. The branches are somewhat fleshy and contorted as well as being very numerous. As stated above, no male florets have yet been found in the ears of the branched corn. Such evidence points to the conclusion that this is not a case of at least total reversion.

As is generally the case in such instances, it is only a matter of conjecture as to the causes that led to the production of this individual which, in so far as is known, was different from all

others in the history of the strain. Mr. W. T. Craig, who has been connected with the corn-breeding work at the University of Illinois for a number of years, states that to his knowledge no ear similar to this has ever been harvested on any of the breeding plots at this station.

The selection in the particular strain in which the branched ear was found has since been discontinued and thus we do not know whether the type would ever have occurred again in the same strain. Hybrid progeny from this parent strain are, however, yet being grown at this station; but no other individuals like the one here described have been found.

Several more generations of the branched corn should be grown before we can make any reliable statements as to its economic value. It is hoped that the new type may be developed by hybridization and subsequent selection among the segregates (which work is in progress now). As yet it does not bear as much grain as the unbranched ear in the strain in which it was found. The parent ear of *Z. ramosa* measured approximately 5.5″ in length and 9″ in circumference. Very little difference was found in the size of the other parts of the plants except that of the tassel, which is also slightly smaller on the new type.

The branched ear is apparently an ideal form to feed whole to livestock. The cob is of such nature that it may be readily masticated with the kernels and without the necessity of grinding or chopping before it is fed. It may also prove to be an ideal type for ensilage. Whether it will yield well enough to justify its production for any of these, or other purposes, remains to be investigated.

NOTES AND LITERATURE

PATTEN ON THE ORIGIN OF VERTEBRATES, AND THE GENERAL QUESTION OF THE VALUE OF SPECULATIONS ON THE PHYLOGENY OF ORGANIC BEINGS[1]

From the standpoint of range of topics covered, amount of work performed, and time devoted to its execution, this work by Patten may without exaggeration be spoken of as monumental. Many of the facts set forth are original observations by the author and his students, and of those not original a large proportion have seemingly been personally studied by him. Furthermore, nearly all the large number of figures are either original or bear the stamp, by way of modification of borrowed figures, of Patten's well-known skill as an illustrator.

A list is appended comprising 26 titles of papers and addresses by the author or the author in collaboration with his students; but unfortunately references to the works of other investigators drawn upon are rather few, often somewhat indefinite, and not well set out in the text. In a book so abounding as is this one in argumentation, many of the main contentions of which are open to debate, sources due to authority ought to be given exactly and without stint.

Frequent as is the occasion in scientific books to estimate worth from the two viewpoints of facts presented and theories defended, rarely is the importance of keeping the two distinct so great as in this case. Many of the chapters, notably V to XII and XVI to XX, are veritable magazines of recorded observation to which workers in the field will, it would seem, find it profitable to turn for years to come. This remark applies particularly to the sections dealing with the central nervous system of *Limulus;* with the cutaneous, olfactory, and optical organs of "Cerachnids" and Anthropods; with the dermal skeleton of *Limulus;* with the endoskeleton of Arachnids; with the nerve

[1] "The Evolution of the Vertebrates and their Kin," by Wm. Patton, 486 pp. and 309 figures, P. Blakiston's Son & Co., 1912.

supply to the heart of *Limulus;* and with the general structure of the Ostracoderms.

The experiments on functions of the brain recorded in Chapter XI should be a valuable contribution to the interesting problem of metamerism as expressed through the activities of the central nervous mechanism.

Two defects in the descriptive matter are likely to interfere with as extensive a utilization of the book by biologists as it merits. The first to be mentioned is a want of directness and definiteness in many of the descriptions that renders their comprehension extremely difficult, in some cases almost impossible. This is due partly to the way references are made to the illustrations. Not infrequently a text description of a structure is given, not very fully, in the course of which one or several figures are referred to but without specifying the letterings for the particular parts described. The reader, being in doubt, may turn to the "Explanation of lettering" at the end of the volume, only to find that the illustrations in question either have no letterings for the particular parts, or if sufficient patience in digging is exercised, to find that the part is labeled with a different name from that used in the description. The account of the "middle cord, the lemmatochord and the notochord" (Chap. XVIII) is an example of the difficulty here indicated. Although I have spent much time on this chapter, I have not been able to get a clear understanding of what is dealt with. How many distinct structures are in hand? "The beginning of the notochord may be recognized in practically all segmented invertebrates, as the so-called middle cord, or median nerve, and in its derivative, the lemmatochord," p. 324. This statement is general, *i. e.,* is not made as applying to any particular animal. It seems definite to the effect that "median nerve" and "middle cord" are synonymous, and that the structure indicated gives rise to the lemmatochord. But Fig. 224*A*, p. 327, representing the "nerve cords and lemmatochord of *Cecropia,*" presents to us the "late pupal stage showing the fully formed lemmatochord, derived from the condensed *sheaths* of the median and *lateral cords;* also remnants of the median nerve." (Italics by the reviewer.) In *Limulus* the "middle cord" is said, p. 334, to be "arranged in two main lateral cords," and Fig. 55, *l.l.ch.,* p. 67, is referred to as illustrating this statement. Turning to this figure and the explanation of letterings, we find that *l.l.ch.* stands

for "lateral bands of the lemmatochord." This same figure shows a "median portion of the lemmatochord" distinctly and widely separated from the lateral portions. The inference is that these lateral and median structures unite somewhere; but no direct statement to this effect is given, at least in the section on the middle cord of *Limulus*.

Again, Fig. 225, p. 328, presents five cross sections of the nerve cord of an adult scorpion. Section 5 is said to show the "merochord." Neither in the description of this figure nor in the text do we find a direct letter reference to the merochord. A structure labeled *m* appears in the figure, but on turning to the explanation of lettering "*m*" we find may stand for "mouth" or "muscle." But it is unfair to criticize illustrations and their letterings and labels alone. They must be taken in connection with the text. By reading a subsection headed "The Bothroidal Cord or Lemmatochord" we find that the merochord in section 5 of Fig. 225 is marked *l.ch.*, which stands for lemmatochord. A sufficiently careful reading of the text clears up the merely expositive difficulties contained in the figure: The merochord is the lemmatochord of the "posterior thoracic neuromeres," p. 328. This interpretation is compelled when Fig. 5 is taken in connection with the text statement indicated. But then the difficulty becomes substantial and not merely expositive, for on page 328 we read: "In the scorpion, the median nerve itself is hardly recognizable. . . . The neurilemmas of the median and lateral cords form the bothroidal cord of the abdomen and the merochord of the posterior thoracic neuromeres." But we have seen above that according to section 5 of Fig. 225 the merochord is a particular part of the lemmatochord. Hence this part at least of the lemmatochord is formed from the neurolemmas of the median and lateral cords. Under the topic "Development of the Lemmatochord" we read "The lemmatochord arises, in part, as an axial cord of cells extending forward from the primitive streak"; and nothing under this heading or elsewhere so far as I have been able to find, harmonizes this statement with the indirect assertion above pointed out that the lemmatochord is formed from the neurilemmas of the median and lateral cords. The nearest approach to such harmonization is the statement, p. 330, that at the time of hatching, the lemmatochord at certain places "remains permanently attached to the neurilemma of the middle cord." As one of the many stu-

dents who have expended considerable time and "gray matter" on the problem of the forerunner of the vertebrate notochord the reviewer would heartily welcome a demonstration that the organ "may be recognized in practically all segmented invertebrates"; but until a clearer, more convincing *description* is furnished us of some structure in "practically all segmented invertebrates" with which the vertebrate notochord is to be compared, the question of homology in the strict sense would not even be raised were the best interests of comparative anatomy duly considered.

The other defect in the presentation of matters-of-fact which a well-wisher for the book may justly fear will tend to prevent as wide use of it as it deserves, is the circumstance that several modes of statement occurring over and over again are bound to give even the fairest-minded reader the impression that many of the facts were prejudged; that is, were collected and recorded not primarily on their merits, but in behalf of a theory. The nomenclature employed in several important connections is likely to have this effect. The use of the substantive *cephalon* with various prefixes in purely descriptive matter dealing with the thoracic region of arthropods is an example.

In the chapter "Minute Structure of the Brain and Cord of Arachnids" we read (p. 80):

> The more posterior thoracic commissures, and those in the hindbrain, are shorter, and the neural and hæmal fascicles are widely separated, leaving a space between them, *which represents the beginning of the fourth ventricle* (italics by the reviewer).

Such dogmatic and uncalled-for statements inserted into purely descriptive matter are very unfortunate, for they can but militate against the factual value of the work in the mind of every candid reader. The feeling of uneasiness engendered in the reader by these gratuitous dogmatizings, as to the extent to which facts dealt with have been unconsciously colored by theory, is not allayed by the author's avowed attitude toward the facts of organic structure. On page 469 we find this:

> Comparative morphology has no value except in so far as it points out the historic sequence of organic forms and functions, and reveals to us the trend of evolution and the causes that direct and control it.

This statement I insist is not true. It may be partly true, but in the unqualified form given it by the author is not only untrue, but is provokingly and harmfully untrue. If for Dr. Patten

comparative morphology has no value except in the ways indicated, well and good. I neither question nor quarrel with the assertion. For me, however, comparative morphology has great value in numerous other ways; and there is much evidence, both historical and contemporaneous, that it has other values for many biologists. It is, I submit, a real even though unintentional harm, not only to individuals, but to biological science, for an able morphologist to make an assertion which carries the clear implication that the interest in and the valuations placed upon comparative morphology by the men who devoted themselves to it long before anybody knew there was such a thing as a "trend of evolution," were an illusory or spurious interest and valuation. And I would express my firm conviction that biologists of this present childhood period of the evolution theory, as the era from Darwin to the present day may well be called, must come to see that great as is the value of morphology as a record of evolution, this is still *only one* of its values; and further, that until such perception is attained, just estimation of the facts of morphology *as a record of evolution* will be impossible. The interest of the future morphologist in his raw material ought to be, according to my understanding, that of the pre-evolutionary morphologist *plus* that growing out of the later discovery that the facts of structure mark the "historic sequence of organic forms and functions." It is just because many, indeed all of the facts dealt with in this work have values for me over and above those attaching to them as a record of evolution that I regret that they could not have been presented in a fashion less calculated to raise doubts in so many instances as to whether they would appear exactly as they do but for the circumstance of having been interpreted by the author in the light of his particular theory of historic sequence.

This consideration will, I trust, give real weight to my words when I say that the criticisms I am passing on Patten's mode of presenting facts is an apology for a work of truly great factual worth, and not at all an attempt to discredit it. Nor would I have any one understand me to be an advocate of "mere facts" of morphology; facts, that is, without any reference to their wider bearings. My point is that all facts of morphology, as of all other departments of biology, have so many "wider bearings" that to write down as without value all except some one set of these bearings, even so important a set as that of evolution, is to narrow the horizon of biological science. Against tenden-

cies of this sort, wherever occurring, and unfortunately they occur in many sections of the vast realm, I am ready at all times to do battle.

So far this review and commentary has been made entirely from the standpoint of observed and observable facts dealt with in the volume. Now the point of view must be shifted to the theoretical side.

Patten's central thesis, as is well known, is that vertebrates have descended from arachnids. The "arachnid theory of the origin of vertebrates," or, for short, the "arachnid theory," is the phraseology used by the author. The theory was first definitely set forth in 1889, the title of the original publication being "On the Origin of Vertebrates from Arachnids." A somewhat abbreviated quotation of the author's outline of the theory will be justifiable. He writes:

> This theory has formed the basis of all my subsequent work, and as far as it went, is practically the same as the one presented here. In that paper it was maintained that the vertebrates are descended from the arachnid division of the arthropods, in which were included the typical arachnids, the trilobites, and merostomes. The ostracoderms were regarded as a separate class, uniting the arachnids with the true vertebrates. *Limulus* and the scorpion were the types most carefully studied, because they were the nearest and most available living representatives of the now extinct merostomes, or giant sea scorpions, that were regarded as the arachnids standing nearest to the ostracoderms.
>
> Other evidence and conclusions were as follows: (1) In the arachnids a forebrain vesicle is formed by the same process of marginal overgrowth as in the vertebrates. . . . (2)The kidney-shaped compound eye of arachnids has been transferred to the walls of the cerebral vesicle in vertebrates, giving rise to the retina, which still shows traces of ommatidia in the arrangement of the rod-and-cone cells. . . . (3) The arachnids have a cartilaginous endocranium similar in shape and location to the primordial cranium of vertebrates. (4) They have an axial, subneural rod comparable with the notochord. (5) In arachnids the brain contains approximately the same number of neuromeres as in vertebrates. . . . (6) The segmental sense organs (median and lateral eyes, olfactory and auditory organs) are comparable with those in vertebrates. The coxal sense organs are associated with special sensory nerves and ganglia, comparable with the cranial dorsal-root nerves and ganglia (suprabranchial sense organs) of verterates. (7) The basal arches of the appendages are comparable with the oral and branchial visceral arches in vertebrates. (8) The tendency toward concentration of neuromeres has narrowed the passage way for the stomodeum and modified the mode of life in the arachnids. This ultimately led to its

permanent closure, the infundibulum and adjacent nerve tissues in vertebrates representing the remnants of the old stomodeum with its nerves and ganglia. . . .[1] (12) The process of gastrulation in vertebrates and arachnids is confined to the procephalic lobes, in the place where at a later period the primitive stomodeum appears. The so-called "gastrulation" of vertebrates and arachnids is an entirely different and independent process, that is, the process of adding by apical or teloblastic growth a segmented, bilaterally symmetrical body to a primitive radially symmetrical head. (13) The arachnids resemble the vertebrates in more general ways, as in the minute structure of cartilage, muscle, nerves, digestive, and sexual organs. (Pp. xvii and xviii of the Introduction.)

None of the statements in this list, either those quoted or those not quoted, bring out clearly one of the most striking features of the theory, namely, the supposition that the ventral surface of the arachnid became the dorsal surface of the vertebrate. This is well shown by several series of figures, as, for instance, that on page eight, of imaginary arthropods and vertebrates with creatures intermediate between them.

During the twenty years and more that the theory has been before zoologists it seems to have won very few adherents; indeed, to have had little influence on biological thinking of any sort. Nor does it seem probable that this final marshaling of the evidence will accomplish much more as regards the main contention. So far are we still from certainty as to exactly how and when the back-boned animals originated that even the probable evidence toward such knowledge is not great. Indeed, if one will consider fully the nature and difficulties of the problem he will see that the chance of ever reaching certainty is almost nil.

What would constitute a demonstration of the parenthood of vertebrates? Obviously the most indubitable proof, that of direct observation, is out of the question. The "supreme canon of historical evidence that only the statement of contemporaries can be admitted," must, in the nature of the case, be completely ignored here. The best chance of reaching a demonstration is in finding a series of fossil animals intermediate between some unmistakably primitive vertebrate and the assumed ancestor, containing no gaps great enough to raise serious doubt in the mind of any competent authority as to the genetic relationship

[1] Number nine in this list is absent in the text. Numbers 10 and 11 are purposely omitted in the quotation.

of the two forms separated by the gap. The greatness of our lack of a series connecting any vertebrate with any invertebrate whatever, must impress one more and more the more he knows and thinks about the problem. The only other conceivable mode of demonstration would be to induce, experimentally, the transformation of some living invertebrate into an undoubted vertebrate. The possibility of accomplishing such a fact is so slight that no biologist is likely to try it.

This brings us to a point where the transcendent importance comes to view, of the logic of the interpretation of evolution, understanding by evolution the transformation of one kind, or species, of organism into another kind, or species. Except in the relatively simple and rare cases of proof through direct observation, experimental or other, the fact that all evidence rests back absolutely on resemblance—on similarity in form and composition of the parts of organisms—is of the utmost importance. No evolutionist hesitates in either word or intention to accept this tenet; yet when it comes to the actual ascertainment of likenesses and differences, and to speculating on their phylogenetic significance, the danger of shifting from the inductive to the deductive mode of reasoning, and of going down before the fallacy known in the logic books as *petitio principii*, or *surreptitious assumption*, is so imminent and subtle that very few of us, even those most wide awake for pitfalls, avoid it wholly. Almost if not quite all the numberless hypothetical ancestral organisms that have been summoned to the aid of speculation on descent during the last half century and more, are, I am convinced, victims of this evil, some in greater, some in less degree. The fallacious reasoning usually runs something like this: Assuming such-or-such an animal once existed, it is easy to see how a particular organ or part of the animal actually before us may have arisen from that ancestry. Says Patten:

> We have merely to strip off the superficial disguise of our hypothetical arachnid ancestors and see whether either their underlying structure, their mode of growth, . . . does or does not harmonize with the assumption that they are the ancestors of the vertebrates (p. 3).

Before this "mere" stripping off begins, would it not be well to consider "our hypothetical arachnid ancestors" rather closely? *If* such an animal actually once existed, let it be granted for the moment that it might have undergone such a transformation as is conjectured. Surely the first point to be pressed is as to the

evidence that the supposed creature did exist. And what is the evidence? Why, the observed facts of arachnid structure, exactly these and no others, else the ancestor would not be held as *hypothetical*. No hypothesis can, of itself, add any new facts. The hypothetical ancestor has, consequently, done nothing for the case except to disguise the obvious difficulty there is in seeing how an *actual* arachnid can be transformed into an *actual* vertebrate.

The only really safe rule for using hypotheses in biology is that no hypothesis shall be made except to help toward answering a question by formulating a clear *provisional* answer to *that question*. The making of hypotheses and using them *before they are themselves proved* for the solution of other problems than those to which they immediately pertain, is perilous business. I may without danger, even with profit, construct an imaginary enteropneust to aid my efforts to answer the question of how the enteropneustic branchial apparatus or the organ in this group called a notochord, arose phylogenetically. But before this imaginary creature can do me real service I must establish at least a strong probability that such an imaginary animal once actually existed. Nor must I fail to notice that such probability can be established only by bringing new evidence into the case. The facts on which I based the hypothetical animal can not be used over again to prove the reality of that animal. But if I must be thus cautious in resorting to an hypothetical enteropneust for the interpretation of actual enteropneusts, how much more need would there be for caution should I venture to invoke an hypothetical enteropneust for interpreting actual vertebrates!

Reflections of this nature opened my eyes several years ago when I was struggling with the enteropneust hypothesis of vertebrate descent, to the very slight chance there is of ever solving the problem of vertebral origin.

Do I then regard all hypotheses on the problem as equal in value because all alike are equally futile? By no means. I consider each one of them to be of real worth, particularly those that have been worked out as have Patten's arachnid hypothesis, Gaskell's crustacean hypothesis, the annelid hypothesis and the enteropneust hypothesis. They are of worth because each shows quite clearly certain *possible* developmental courses that may have been followed in the origin and progress of the great vertebral stock. To be explicit, it seems to me that Patten has shown

that in certain structural details there is a similarity between the exoskeletons of *Limulus* and some of the Ostrachoderms which makes quite possible, not somewhat probable, genetic relationship between these animals. Similarly the remarkable likeness between the gills of the enteropneust and amphioxus, if considered by itself, would make genetic kinship between these animals highly probable; however, when considered along with the whole organization and mode of life of each group, the probability is much reduced, to such an extent, indeed, as to become hardly more than a strong possibility.

If we take due cognizance of the extent to which our faith in the general theory of organic evolution rests on similarities of form and function among individual organisms which come under our observation, we are in position to feel the weight of the purely inductive evidence furnished by the many resemblances between vertebrates and invertebrates brought to light by the investigators in support of the various hypotheses of vertebrate ancestry, that not only is the theory of evolution true as applied to the back-boned animals, but that the ancestors of these animals must have been in many respects like certain invertebrated animals with which we are familiar. The inductive proof of the truth of organic evolution, even of the general course of evolution within large provinces of the living world, approaches much closer to certainty when taken *en masse* than does, of necessity, that pertaining to any single instance or small group of instances.

So the moral drawn from examining the theoretical side of the volume before us has this in common with that drawn from examining the factual side: It has real worth, but that worth would stand forth much more sharply, and probably would be received by biologists with far greater sympathy, had it been always and clearly distinguished in presentation from pure matters of fact. And the worth would have been greater still had the main and numerous subsidiary and corollary hypotheses been frankly treated as far from demonstrated or even demonstrable, but as varying in degree of reasonableness from very *possibly* true to rather *probably* true.

WM. E. RITTER

LA JOLLA, CALIF.,
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